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A revision of the southeast Asian freshwater crabs of the genus *Isolapotamon* Bott, 1968 (Crustacea: Decapoda: Brachyura: Potamidae)

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Abstract.—The taxonomy of the potamid freshwater crab genus *Isolapotamon* Bott, 1968, is revised. Fifteen Bornean species (including two new ones) and three Philippine species are recognized. The fifteen Bornean species are: *I. anomalum* (Chace, 1938) (type species), *I. bauense* Ng, 1987, *I. beeliae* Ng, 1986, *I. borneense,* new species, *I. collinsi* Holthuis, 1979, *I. consobrinum* (De Man 1899), *I. doriae* (Nobili 1900), *I. griswoldi* (Chace, 1938), *I. grusophallus* Ng & Yang, 1986, *I. ingeri,* new species, *I. kinabaluense* (Rathbun, 1904), *I. mahakkamense* (De Man, 1899), *I. naiadis* Ng, 1986, *I. nimboni* Ng, 1987, and *I. stuebingi* Ng, 1995. The three Philippine species are: *I. mindanaoense* (Rathbun, 1904), *I. sinuatifrons* (H. Milne Edwards, 1853) and *I. spatha* Ng & Takeda, 1992. These species are distinguished mainly by means of their gonopodal and carapace features.

The family Potamidae is represented by three genera in the island of Borneo (Brunei, Malaysian Sarawak and Sabah, and Indonesian Kalimantan), i.e., *Isolapotamon* Bott, 1968, *Cerberusa* Holthuis, 1979, and *Ibanum* Ng, 1995. *Cerberusa* contains only two troglobitic species, known only from the caves in northern Gunung Mulu Sarawak (Holthuis 1979). *Ibanum* contains two non-troglobitic species, one from central Kalimantan and the other from Sarawak (Ng 1995). *Isolapotamon* is the largest genus, with 13 described species (Bott 1970b, Ng 1986, 1987, 1995). Three other species are known from the island of Mindanao in the southern Philippines (Bott 1970b, Ng & Takeda 1992).

Bott (1970b) included *Isolapotamon*, *Malayopotamon* Bott, 1968, and *Nanhaipotamon* Bott, 1968, in a new family, Isolapotamidae, which he defined as having stout or elongate male first pleopods, and whose members presumably occurred mainly in Sumatra, Java, Borneo and the Philippines, with some species present in Taiwan, southern China and Peninsular Malaysia. The Isolapotamidae, however, lacks sufficient distinguishing characters from typical potamids to warrant its recognition as a separate family (Ng 1986, 1987, 1988a, 1988b; Ng & Yang 1985, 1986). None of the three genera in the Isolapotamidae (*Isolapotamon*, *Malayopotamon* and *Nanhaipotamon*) possess characters unique to themselves. Substantial changes have also occured with the discovery of additional Sundaic species of, for example *Cerberusa* and *Ibanum* and clarification of various genera such as *Nanhaipotamon* (see Ng & Dudgeon 1992, Ng & Takeda 1992, Dai & Ng 1994, Dai 1997), which casts serious doubts on the validity of the Isolapotamidae. In this paper, the genus *Isolapotamon* is revised and placed in the family Potamidae Ortmann, 1896 (sensu Ng 1988a).

All measurements, in millimeters, are included as carapace widths by lengths. The terminology used follows that used by Ng (1988a). Specimens are deposited in the Museum of Comparative Zoology, Harvard

University (MCZ); National Museum of Natural History (USNM), Washington, D.C; National Natuurhistorische Museum (former Rijksmuseum van Natuurlijke Historie), Leiden (NNM); The National History Museum, London (NHM); Museum Civico di Storia Naturale, Genoa (MGE); Museo ed Istituto di Zoologia Sistematica della Universita di Torino, Turin (MUT); National Science Museum, Tokyo (NSMT); Zoological Reference Collection, School of Biological Sciences, National University of Singapore (ZRC); Museum of Zoology, Cambridge University, (CMZ); Muséum National d'Histoire naturelle, Paris (MNHN); Sarawak Museum, Kuching (SM); and the Museum Zoologicum Bogoriense, Bogor (MZB).

The abbreviations G1 and G2 are used for the male first and second pleopods respectively; Mt. and Sg., for Mount and Sungai respectively, the latter term meaning river in Malay. Altitudes above sea level are indicated in meters (m). Localities of collecting sites have been derived from Anon (1971) or from the field collector's data.

Taxonomy

Family Potamidae Ortmann, 1896

Genus *Isolapotamon* Bott, 1968

Isolapotamon (Isolapotamon) Bott, 1968: 119.

Isolapotamon.—Bott, 1970a:333; Bott, 1970b:190.

Diagnosis.—Carapace broader than long; epigastric and postorbital cristae well developed, separate; anterolateral margin convex, serrated; external orbital angle usually broadly triangular, outer margin distinctly longer than inner margin; epibranchial tooth present. Exopod of third maxilliped very broad, especially proximally, outer margin distinctly convex outwards; distal tip reaches or slightly exceeds half length of merus; flagellum distinct, longer than width of merus. Male abdomen distinctly triangular, lateral margins of last segment convex or almost straight; telson triangular. G1 slender, elongated; terminal segment subequal to or longer than subterminal segment, slender, tip often dilated. G2 slender, elongated; distal segment distinct, subequal to half length of basal segment.

Type species.—*Potamon anomalus* Chace, 1938, by original designation.

Remarks.—Bott (1968) erected *Isolapotamon* with three subgenera, i.e. *Isolapotamon*, *Malayopotamon* Bott, 1968, and *Nanhaipotamon* Bott, 1968. Bott (1970a) subsequently raised all three to distinct genera and placed them in a new family, the Isolapotamidae (Bott 1970b), recognising eight species in the genus *Isolapotamon*. Bott (1970b) also excluded the Philippine species "*Telphusa artifrons* Bürger, 1894," which he had earlier (1968) placed in *Isolapotamon* (*Isolapotamon*), and referred it to the genus *Tiwaripotamon* Bott, 1970. Ng (1992) reviewed the problems associated with Bott's genus *Tiwaripotamon*, and subsequently Ng & Takeda (1992) established a new genus, *Ovitamon*, for Bürger's species as well as two new species from the Philippines.

Bott (1970b) placed *Potamon* (*Potamiscus*) *chaseni* Roux, 1934, in the genus *Isolapotamon*, noting that it was the only member of the genus from Peninsular Malaysia. *Isolapotamon chaseni* differs from typical *Isolapotamon* species in at least one very major character, the form of the exopod of the third maxilliped. In the Bornean and Philippine *Isolapotamon*, the exopod of the third maxilliped is very broad, especially proximally, and the outer margin is distinctly convex outwards. When the exopod is appressed against the endopod, the outer margin of the third maxilliped has a rounded appearance. This type of third maxilliped exopod is known in only one other sundaic taxon, *Allopotamon tambelanense* (Rathbun, 1905), from the Tambelan Islands west of Borneo (Ng 1988b). In *I. chaseni*, the exopod is proportionately more narrow, the outer margin being almost straight or only slightly convex, giving the third maxilliped a more quadrate appearance (see Ng 1988).

The structure of the G1 of *I. chaseni*, and the absence of a flagellum on the third maxilliped exopod, suggests that this species should be excluded from the genus *Isolapotamon*. Ng (1988b) referred this species to the Malayan genus *Stoliczia* Bott, 1966.

Seven *Isolapotamon* species have been described from China, viz. *I. sinense* Tai & Sung, 1975, *I. papilionaceum* Dai, Song, He, Cao, Xu & Zhong, 1975, *I. physalisum* Dai, Song, Li, Chen, Wang & Hu, 1984, *I. aflagellum* Dai, Song, Li & Liang, 1980, *I. nasicum* Dai, Chen, Song, Fan, Lin & Zeng, 1979, *I. sheni* Dai, Chen, Liu, Luo, Yi, Liu, Gu & Liu, 1990, and *I. obtortum* Dai, Song, Li, Chen, Wang & Hu, 1984. All these Chinese *Isolapotamon* species, however, have the exopod of the third maxilliped slender (not broad) and the outer margin being straight (not convex outwards). In addition, the G1 terminal segment of the Chinese species is proportionately much longer than the subterminal segment, where as it is equal to or more than half the length of the subterminal segment in *Isolapotamon*. In a recent reappraisal of these species using the above features as well as the structures of the external orbital angle, exopod of the third maxilliped, male abdomen and G1, Dai & Türkay (1997) referred the Chinese species to four new genera, viz. *Neilupotamon*, *Yarepotamon*, *Minpotamon*, *Vadosapotamon* and *Latopotamon*. As a result of this, *Isolapotamon* s. str. has a wholly Bornean and Philippine distribution.

The form of the exopod of the third maxilliped exopod in *Malayopotamon* and *Nanhaipotamon* is very different from that of *Isolapotamon*. Examination of *Malayopotamon* and *Nanhaipotamon* specimens shows that, like other Southeast Asian potamids, their exopods are slender and the outer margins slightly concave. This observation, together with the fact that the G1s of the three genera are markedly different, indicates that the three genera are not closely related, contrary to Bott's (1970b) belief.

The generic diagnostic characters defined by Bott (1968) for *Isolapotamon* are generally valid and are used here in a modified form. Ng (1986, 1987) and Ng & Yang (1986) partially revised the genus, adding five new species to the Bornean fauna and resurrecting another species which Bott (1970b) had synonymised with *I. mahakkamense* (De Man, 1899). A total of 15 Bornean species are now recognized, two of which are here described as new: *I. anomalum* (Chace, 1938) (type species), *I. bauense* Ng, 1987, *I. beeliae* Ng, 1986, *I. borneense*, new species, *I. collinsi* Holthuis, 1979, *I. consobrinum* (De Man, 1899), *I. doriae* (Nobili, 1900), *I. griswoldi* (Chace, 1938), *I. grusophallus* Ng & Yang, 1986, *I. ingeri*, new species, *I. kinabaluense* (Rathbun, 1904), *I. mahakkamense* (De Man, 1899), *I. naiadis* Ng, 1986, *I. nimboni* Ng, 1987, and *I. stuebingi* Ng, 1995.

Although the present paper deals essentially with Bornean potamids, three poorly known Philippines species, *I. mindanaoense* (Rathbun, 1904), *I. sinuatifrons* (H. Milne Edwards, 1853) and *I. spatha* Ng & Takeda, 1992, are also discussed for completeness.

Key to the Species of *Isolapotamon*

1a. Carapace relatively deep, carapace height to width ratio 0.4–0.5; G1 terminal segment about equal to subterminal segment, terminal segment sinuous, tip dilated, forming a right-angled triangular projection (Fig. 1E–H) (Sarawak) ..... *I. bauense*

1b. Carapace normal or flat, carapace height to width ratio distinctly less than 0.4; G1 terminal segment equal or subequal to subterminal segment, terminal segment sinuous or straight, tip dilated, laterally flattened, rounded, or with a secondary projection 2

2a. Dorsal surface of carapace evenly flat; epibranchial tooth distinct, well developed, separated from the anterolateral margin by distinct triangular cleft ... 3

2b. Dorsal surface of carapace inflated or only inflated in 1 or 2 regions; epibranchial tooth indistinct or distinct

but separated from anterolateral margin by shallow cleft 4

3a. Carapace wider than long to almost squarish (Fig. 3), dorsal surfaces smooth; anterolateral regions striated; intestinal region smooth; epibranchial tooth well developed, tip sharp, separated from anterolateral margin by deep, distinctly triangular cleft; epigastric cristae sharp; G1 terminal segment tip dilated to form "knob-like" structure or appearing vaguely triangular (Figs. 5E–H) (Sarawak, northwestern Kalimantan) .... *I. consobrinum*

3b. Carapace wider than long, dorsal surfaces rugose, especially anterolateral and posterolateral regions; intestinal regions granulose; epibranchial tooth prominent but tip not sharp, separated from anterolateral margin by relatively shallower triangular cleft; epigastric cristae rugose; G1 terminal segment tip not dilated or rounded (Fig. 12E–H) (Sarawak, northwestern Kalimantan) ..... *I. stuebingi*

4a. Dorsal surface of carapace granulated, especially on anterolateral, posterolateral, epigastric, postorbital, branchial and intestinal regions (Fig. 9); epigastric cristae rugose but low; posterolateral margins distinctly convex; outer margin of external orbital angle about 4 times longer than inner margin; cervical groove shallow; no groove discernible between cardiac and intestinal regions; G1 not known (central Kalimantan) ..... *I. mahakkamense*

4b. Dorsal surface of carapace granulated or striated only on anterolateral and/or posterolateral regions; epigastric cristae not rugose, distinct and usually prominent; posterolateral margins straight to concave; external orbital angle about 2 or 3 times longer than internal orbital angle; cervical groove shallow or deep, groove between cardiac and intestinal region present or absent; G1 straight to or sinuous ... 5

5a. Epigastric cristae distinct, sloping from centre and merging gradually with postorbital cristae; dactylus of last ambulatory leg very short; G1 sinuous, terminal segment subequal in length to subterminal segment, distal part bifurcated, subdistal process subequal in length to distal process (Fig. 5M–P) (Sabah) ..... *I. griswoldi*

5b. Epigastric cristae indistinct, distinctly separated from postorbital cristae by wide, disjunct notch; dactylus of last ambulatory leg long or medium lengthed; G1 sinuous to almost straight, terminal segment of varying lengths, distal part of various forms 6

6a. G1 slightly sinuous to almost straight, not distinctly sinuous, tip forming head-like structure or bifurcated 7

6b. G1 very slender, distinctly sinuous, tip rounded, forming "knob-like" structure 14

7a. Distal part of G1 terminal segment forming a "head-like" structure 8

7b. Distal part of G1 terminal segment bifurcated 16

8a. Tip of distal part of G1 terminal segment distinctly rounded, outer margin of dilated part gradually curving to meet cylindrical part of terminal segment, inner margin of distal part curving gradually without distinct hump 9

8b. Tip of distal part of G1 terminal segment not rounded, usually trapezoidal or triangular, outer margin of dilated part gradually curving to meet cylindrical part of terminal segment, inner margin of distal part curving gradually with or without distinct hump 11

9a. Distal part of G1 terminal segment at right angles to the G1, forming an inverted "boot-like" structure (Figs. 10M–P) (Mindanao) ..... *I. sinuatifrons*

9b. Distal part of G1 terminal segment not at right angles, usually directed at 45° to the perpendicular, forming a "knob-like" structure 10

10a. G1 tip dilated, twice as long as broad (Fig. 10A–D) (Mindanao) ..... *I. mindanaoense*

10b. G1 tip dilated, as long as broad (Fig. 12A–D) (Mindanao) ..... *I. spatha*

11a. G1 gently sinuous, especially terminal segment, tip resembling a "chicken head" (Figs. 1M–P) (Sarawak ?) ..... *I. borneense*

11b. G1 almost straight, terminal segment

tip dilated, trapezoidal or triangular, not resembling a "chicken head" ... 12

12a. G1 subterminal segment with distinct notch at proximal end, terminal segment tip dilated, rounded, forming a "club-like" structure (Fig. 8) (Sabah) ..... *I. kinabaluense*

12b. G1 subterminal segment without distinct notch at proximal end, terminal segment tip dilated, flattened, forming a "horse head-like" structure 13

13a. Distal side of G1 tip longer than proximal side (Fig. 1A–D) (Sabah) ..... *I. anomalum*

13b. Distal side of G1 tip shorter than proximal side (Figs. 6E–H) (Sabah) .. *I. ingeri*

14a. G1 terminal segment distinctly longer than subterminal segment, tip evenly rounded (Fig. 5I–L) (Sarawak) .. *I. doriae*

14b. G1 terminal segment subequal to or slightly longer than subterminal segment, distal part unevenly dilated, upper margins gently convex to almost straight 15

15a. Outer part of dilated G1 terminal segment tip projecting slightly outwards, upper margin gently convex, curving gently downwards about 90° to form dilation (Fig. 10E–H) (southeastern Kalimantan) ..... *I. naiadis*

15b. Dilated part of distal part of G1 terminal segment almost triangular, upper margin almost straight, sloping downwards sharply (Fig. 1I–L) (southeastern Kalimantan) .... *I. beeliae*

16a. Subdistal process of distal part of G1 terminal segment twice as long as distal process (Fig. 6A–D) (Sarawak) .. .. *I. grusophallus*

16b. Subdistal process of distal part of G1 terminal segment subequal in length to distal process 17

17a. Distal and subdistal projections of distal part of G1 terminal segment meeting at right angles at outer margin, distal process approximately equal in length to subdistal process (Fig. 10I–L) (Sarawak) ..... *I. nimboni*

17b. Distal and subdistal projections of distal part of G1 terminal segment meeting gradually (sloping) at outer margin, subdistal process appears longer (but less than 1.5 times) than distal process (Fig. 5A–D) (Sarawak) ..... *I. collinsi*

Isolapotamon anomalum (Chace, 1938)
Fig. 1A–D

Potamon anomalus Chace, 1938:14, pl. 2.

Potamon (*Potamon*) *anomalus*.—Yang, 1979:17.

Isolapotamon (*Isolapotamon*) *anomalum*.—Bott, 1968:120, fig. 1.

Isolapotamon anomalum.—Bott, 1970b: 191, pl. 41 fig. 77, pl. 56 fig. 82.

Stoliczia leoi.—Ng, 1988b: fig. 35A, B (not *Potamiscus leoi* Ng & Yang, 1985).

Material examined.—Paratypes, 1 male (34.2 by 26.3 mm), 1 female (27.4 by 21.6 mm) (ZRC 1990.461–462), Borneo, Sabah: Mount Kinabalu, Bundutan (Bundu Tuhan), Luidan River, ca. 5°58′N, 116°32′E, coll. J. A. Griswold Jr., 11 Jul 1937. Paratypes, 2 males (dry) (USNM 075896), Borneo, Sabah, coll. Asiatic Primate Expedition, 11 Jul 1937. Others—2 males, 1 female, 2 juveniles (largest 27.2 by 20.9 mm) (ZRC 1990.3641–3645), Borneo, Sabah: stagnant pools, Sg. Mengalum, Mendolong, ca. 4°45′N, 115°40′E, Sipitang District, coll. R. B. Stuebing, 8 Aug 1989. 2 males, 2 females (USMN 96334), North Borneo: Tenompok, stn. 27, coll. B. C. Walton, 25 Mar 1954.

Diagnosis.—Carapace dorsal surface smooth; anterolateral margins convex, not distinctly cristate; epibranchial regions striated, striae low; postorbital and epigastric ridge low; epibranchial tooth low, blunt; external orbital angle triangular, distinctly behind frontal margin. Dactylus of last ambulatory leg long. G1 sinuous, subdistal process truncate, forming "horse head-like" structure.

Remarks.—Bott (1968) recorded this species from the Luidan River, at an altitude of 1000 m above sea level. This is one of the three species of *Isolapotamon* in the Kinabalu area of Sabah. *Isolapotamon anomalum* is easily distinguished from *I. griswoldi* by having a proportionately longer dactylus on the last ambulatory leg. *Isolapotamon anomalum* resembles *I. kinabaluense* with regards to the long dactylus of

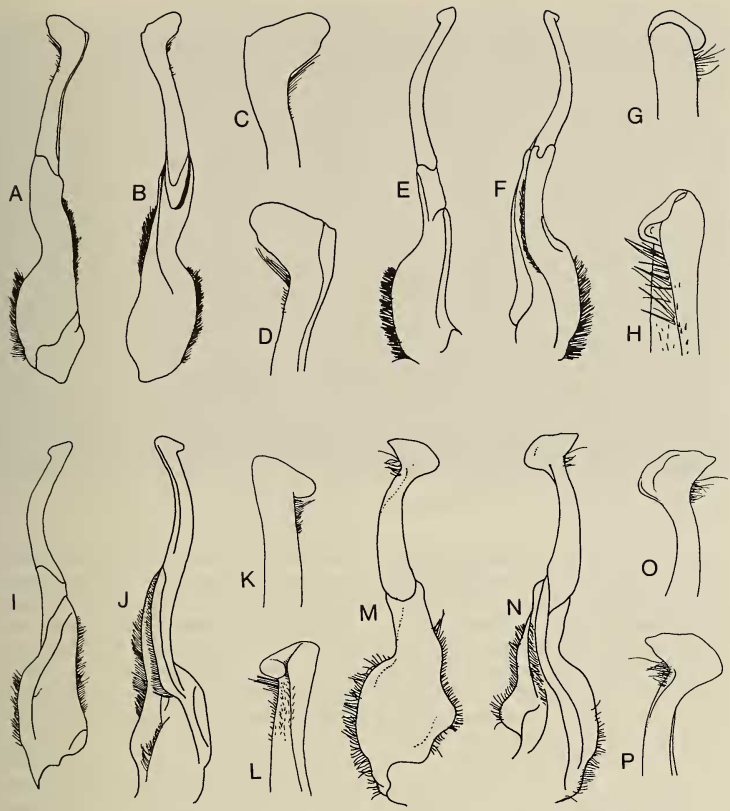

Fig. 1. G1s. A–D: *I. anomalum*, paratype male (ZRC 1990.461); E–H: *I. bauense*, holotype male (SM Cru Nr. 1986.9) (after Ng, 1987); I–L: *I. beeliae*, holotype male (MZB Cru Nr. 464) (after Ng, 1986); M–P: *I. borneense*, holotype male (ZRC 1984.7042). A, E, I, M: dorsal view; B, F, J, N: ventral view; C, G, K, O: dorsal view, tip of terminal segment; D, H, L, P: ventral view, tip of terminal segment.

the last ambulatory leg. In adult specimens of *I. anomalum*, the striae on the epibrachial regions are very low. This makes the crab appear smooth on the dorsal surface of the carapace. The smoother carapace and "horse-head" distal part of the G1 terminal segment easily distinguishes *I. anomalum* from *I. kinabaluense*.

The postorbital and epigastric ridge is remarkably low in adult specimens. It is also not distinctly cristate. In juveniles, both ridges are distinct and cristate.

The figures of the carapace supposedly of "*Stoliczia leoi*" published in Ng (1988b: fig. 35A, B) do not belong to that species but to *Isolapotamon anomalum* (Chace,

1938) instead. The incorrect negatives were accidentally printed. The correct photographs of *Stoliczia leoi* are depicted in the original description of the species by Ng & Yang (1985). The figures of the gonopods and mouthparts of *S. leoi* in (Ng 1988b: fig. 35C–G), however, are correct.

Isolapotamon bauense Ng, 1987
Fig. 1E–H

Isolapotamon (*Isolapotamon*) *mahakkamense*.—Bott, 1968:120 (part), fig. 7a, b (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon mahakhamense.—Bott, 1970b: 193 (part), pl. 41 fig. 81, pl. 56 fig. 81 (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *mahakkamense*.—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon bauensis Ng, 1987:145, fig. 3A–E, pls. 8, 9.

Material examined.—Holotype, male (66.3 by 51.0 mm) (SM Cru Nr. 1986.9), Borneo, Sarawak: Serian, cave stream, in total darkness, Lobang Siri, Gua Siri Paya (Kampong) Bentang, 27 miles, ca. 1°22′N, 110°09′E, coll. Lord Medway, 10 Dec 1957. Paratype, 1 male (62.5 by 49.0 mm) (SM Cru Nr 1986.10), same data as holotype. 1 male (85.1 by 61.8 mm) (SM Cru Nr 1986.3), Borneo, Sarawak: Bidi Caves, Bau district, ca. 1°23′N, 110°06′E, coll. C. J. Brooks, Jun 1903. 1 male (71.0 by 53.1 mm), 1 female (58.2 by 42.9 mm) (NHM 1911.2.3.1–2), Borneo: Bidi, Upper Sarawak, coll. C. J. Brooks. 1 male (71.0 by 53.1 mm), 1 female (58.2 by 42.9 mm) (NHM 1911.2.3.1–2), Bidi, upper Sarawak, presented by C. J. Brooks. 1 male (ZRC 1997.782), Borneo, Sarawak: Serian, Gua Sireh, coll. Charles Leh & Mahmuad, Oct 1982.

Diagnosis.—Carapace high, but dorsal surfaces flat, surfaces rugose, epigastric and postorbital cristae low but visible, anterolateral margins very convex, distinctly serrated, epibranchial tooth very small, external orbital angle broadly triangular, margin straight or slightly convex, serrated. Dactylus of last ambulatory leg long. G1 long, slender, sinuous, terminal segment sinuous, tip slightly dilated on outer margin of distal part.

Remarks.—Bott (1968, 1970b) referred several specimens from the Bau district of Sarawak to *I. mahakkamense*, a species originally described from a single large female from the upper stretches of the Mahakkam river, a locality which is 340 km from Bau. Ng (1987), however, showed that two separate taxa were involved, and established a new species, *I. bauensis*, for the Sarawakian specimens.

The locality of the holotype should be Serian (not Senian). This is a small town east of Bau and Kuching. Bau (locality of the paratype) is to the west of Kuching. The specific name should be "bauense" as the genus *Isolapotamon* is neuter. The details of its taxonomy can be found in Ng (1987). *Isolapotamon bauense* is probably the largest known potamid, indeed the largest known freshwater crab, from Southeast Asia, with the largest specimen measuring 85.1 by 61.8 mm (SM Cru Nr 1986.3).

The form and ornamentation on the carapace of *I. bauense* appears to vary somewhat. A heterosexual pair of specimens of *I. bauense* from Bidi (NHM 1911.2.3.1–2) closely resemble *I. mahakkamense* superficially, especially with regards to the finely granulated dorsal surface of the carapace (rugose in the types of *I. bauense*). The G1 of the male specimen, however, is identical to that of the holotype of *I. bauense*. In addition, we have discerned three additional non-sexual differences which can serve to separate *I. bauense* from *I. mahakkamense*. Firstly, in *I. bauense*, the distal part of the third maxilliped exopod tapers gradually, giving it a subcylindrical appearance, whilst in *I. mahakkamense*, however, it tapers sharply, with the structure appearing distinctly acute. Secondly, the frontal margin of *I. bauense* is also entire, whereas in *I.*

Fig. 2. *Isolapotamon borneense*, new species. Holotype male (32.0 by 23.6 mm) (ZRC 1984.7042).

mahakkamense, the median lobes are separated from the lateral lobes by a distinct notch. Thirdly, the median lobe of the posterior margin of the epistome in *I. bauense* is evenly triangular in shape with the lateral margins almost straight, whereas in *I. mahakkamense*, the lateral margins are concave, with the distal part and tip appearing elongate.

Isolapotamon beeliae Ng, 1986
Fig. 1I–L

Isolapotamon beeliae Ng, 1986:219, figs. 3, 4.

Material examined.—Holotype, male (61.0 by 44.9 mm) (MZB Cru Nr. 464), Borneo, Kalimantan: Alai R. Datar, Barabai, Meratus Mountains, 2°36′44″S, 115°22′02″E, coll. M. A. Rifai, 22 Oct 1972.

Diagnosis.—Carapace tranverse, postorbital cristae straight, parallel with the frontal margin. Dactylus of last ambulatory leg long. G1 terminal segment sinuous, slightly shorter than subterminal, with short but distinct subterminal process.

Remarks.—Ng (1986) described this species on the basis of a single large male from Barabai in southern Kalimantan, but the G1 of *I. beeliae* is very distinct and hence easily separated from all known congeners. The details of its taxonomy and affinities with other *Isolapotamon* have been discussed in detail by Ng (1986).

Isolapotamon borneense, new species
Figs. 1M–P, 2

Material examined.—Holotype, male (32.0 by 23.6 mm) (ZRC 1984.7042), Borneo, probably Sarawak, no other data.

Diagnosis.—Carapace wider than long, postorbital cristae subparallel with frontal margin. Dactylus of last ambulatory leg long. G1 terminal segment gently sinuous, subequal to subterminal segment, with "chicken head-like" structure.

Description.—Carapace wider than long, surface flat, smooth with numerous small

pits; anterolateral margins convex, gradually merging with posterolateral margins; posterolateral margins straight, converging towards posterior margin, posterior margin straight; gastric, branchial, intestinal regions slightly inflated, epigastric groove distinct, cervical groove prominent, H-shape depression strong; epigastric region sparsely granulated, epigastric cristae distinct, slightly in front of postorbital cristae, subparallel to frontal margin, epigastric lobes trapezoidal; postorbital cristae prominent, subparallel to frontal margin, not confluent with epigastric cristae, confluent with epibranchial teeth base; frontal margin raised, forming cristae anteriorly, sinuous, about 0.3 of carapace width, forming four lobes, each median lobe about 1.5 times wider than a lateral lobe; outer orbital angle broad. Anterolateral margin evenly carinate, striated, distinct epibranchial incision. Eyes well developed; supra- and infraorbital cristae prominent, granulated; suborbital regions sparsely granulated. Pterygostomial region striated. Median frontal triangle absent.

Third maxillipeds covering entire oral field, except efferent opening; ischium with longitudinal median groove; exopod with well developed flagellum.

Chelipeds unequal, merus ventral surface with two distinct cristae, anterior cristae distinctly granulated, posterior cristae less granulated; frontal surface of cheliped with numerous pits, inner surface of palm smooth, about 5–6 low ridges on lower part of pollex, finger with 5–6 shallow grooves.

Ambulatory legs normal, merus without subterminal spine, second pair longest, dactylus of last pair long.

Holotype male abdomen triangular and elongate, widest at third segment, narrows gradually towards telson.

G1 gently sinuous, terminal segment about equal to subterminal segment; terminal segment tip enlarged, shaped like a "chicken head." G2 sinuous, bent at two points, one at joint between subterminal and terminal segment, the other at proximal one-third of terminal segment, tip pointed. Terminal segment slightly shorter than subterminal segment.

Remarks.—The exact locality where the holotype and only known specimen of this species was collected is uncertain. It was found in a sealed bottle, without any data, with specimens of *Stygothelphusa bidiense* (Lanchester, 1900), a gecarcinucid species known only from the Bau area in western Sarawak. It is possible that the specimen was obtained from or near that site (see Ng 1989a). *Isolapotamon bauense* Ng, 1987, also described from the Bau area, has a very different carapace physiognomy and G1 structure compared to *I. borneense*.

The provenance of the present specimen poses some problems as it is not known from which part of Borneo it was obtained. Considering that prior to the mid-1980s, all the ZRC material from Borneo came from either Sarawak or Sabah, it seems likely that the present specimen of *I. borneense* is from either of these two states. As all the specimens in ZRC from Sabah have been reported in the literature (with no species fitting description of *I. borneense*), there is a good chance that the type specimen was in fact obtained from somewhere in Sarawak.

The G1 of the *I. borneense* is very distinctive and quite unlike any *Isolapotamon* species described thus far. The "chicken head-like" distal part of the terminal segment bears some similarity to that of *I. griswoldi*, *I. kinabaluense* and *I. anomalum*, but *I. borneense* can easily be separated by its terminal segment being very sinuous (only slightly sinuous in *I. griswoldi* and almost straight in *I. kinablauense* and *I. anomalum*). The long dactylus of the last ambulatory leg of *I. borneense* also distinguishes it from *I. griswoldi*.

Etymology.—Named after the island of Borneo.

Isolapotamon collinsi Holthuis, 1979
Fig. 5A–D

Isolapotamon collinsi Holthuis, 1979:21, pl. 4, fig 4.

Isolapotamon collinsi.—Holthuis, 1986: 593; Ng, 1987:147, fig. 3F; Guinot, 1988: 13.

Material examined.—Holotype, male (56.0 by 40.0 mm) (NNM), Borneo, Sarawak: Gunong Mulu National Park, Hidden Valley, Sinkhole of Clearwater River next to camp 6, coll. P. Chapman, 27 Mar 1978. Paratype, male (50.0 by 35.0 mm) (NNM), same data as holotype. Others—2 females (ZRC 1997.795), Borneo, Brunei: tributary of Sg. Temburong, near plot 2, East Ridge, at night, coll. I. Das, 23 Apr 1992. 2 females, 2 juveniles (ZRC 1997.794), Borneo, Brunei: Belalong, Sg. Engkabang, coll. S. Choy, 8 Feb 1991. 1 male, 3 juveniles (ZRC 1997.793), Borneo, Brunei: Temburong, Sg. Belalong at Kuala Belalong, coll. K. Lim et al., 14–17 Jun 1995. 1 male (NHM 1928.12.1.84), Borneo, Sarawak: Kuching, Stebbing Collection, coll. C. Hose.

Diagnosis.—Carapace flat, surfaces rugose, especially on anterolateral, posterolateral and gastric regions; epibranchial tooth low but distinct, with distinct notch separating it from external orbital angle; anterolateral margins gently serrated, external orbital angle broadly triangular. Surfaces of chelipeds and ambulatory legs rugose. Dactylus of last ambulatory leg long. G1 sinuous, terminal segment sinuous, tip bifurcated, subdistal process subequal or slightly longer than distal process.

Remarks.—The structure of the G1 of *I. collinsi* allies it with species like *I. griswoldi*, *I. grusophallus* and *I. nimboni*. The taxonomy and biology of this species has been well documented by Holthuis (1979). It was described from from two specimens, but we have examined some specimens from Brunei and Sarawak which agree with the types well. The G1s of the specimens have a thicker thumb-like projection and are gently curved outwards than that figured in Holthuis (1979). The distal projection of the terminal segment is also slightly thicker when compared to that figured by Holthuis (1979). However, the angle produced between the tip and the thumb-like projection is more than right angles. This character can be used to easily distinguish *I. collinsi* from *I. nimboni* (see remarks under *I. nimboni*). A specimen collected from Kuching (NHM 1928.12.1.84) was incorrectly identified as *I. mahakkamense*. The G1 of this specimen is very similar to that illustrated by Holthuis (1979) and there is no doubt that it is conspecific with *I. collinsi*.

With regards to its habits, Ng (1987) commented that in all likelihood, *I. collinsi* is a troglophile like *I. bauense*. All the Bruneian specimens of *I. collinsi* were collected from fast flowing streams not associated with caves.

One specimen (NHM 1928.12.1.84) is noteworthy as it was supposedly obtained from Kuching. The present study has shown that all *Isolapotamon* specimens examined thus far from Kuching and western Borneo are either *I. consobrinum* or *I. bauense*, with *I. collinsi* found only in northeastern Sarawak and Brunei. The NHM specimen is, however, clearly conspecific with *I. collinsi*. There is another specimen (NHM 1928.12.1.83) from the same lot as this one and it is *I. consobrinum*, which is known from the Kuching area. We therefore suspect that the locality data for the specimen of *I. collinsi* is incorrect, and it was actually collected much further north. In the earlier part of this century, many specimens from Sarawak were simply labelled as being from the main city, Kuching, even though they had been collected further afield (see Ng 1989b).

Isolapotamon consobrinum
(De Man, 1899)
Figs. 3, 5E–H

?*Telphusa sinuatifron.*—Miers, 1880:305 (not *Potamon sinuatifrons* H. Milne Edwards, 1853).

Potamon (*Potamon*) *consobrinus* De Man,

Fig. 3. *Isolapotamon consobrinum*. Lectotype male (45.0 by 33.0 mm) (NNM Cru Nr. 1299).

1899: 99 (part), pl. 9 fig. 10b, f, pl. 10 fig. 10.

Potamon (*Potamon*) *mahakkamense*.—Nobili, 1903b:14 (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *mahakkamense*.—Rathbun, 1904:268 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *consobrinus*.—Rathbun, 1904:269 (part).

Potamon (*Potamon*) *consobrinus*.—Yang, 1979:17.

Isolapotamon (*Isolapotamon*) *consobrinum*.—Bott, 1968:121, fig. 4a, b.

Isolapotamon consobrinus.—Bott, 1970b: 194, pl. 41 fig. 82, pl. 56 fig. 83.

Potamon (*Potamon*) *consobrinum*.—Leh, 1982:4.

Potamon (*Potamon*) *mahakkamense*.—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon consobrinum.—Ng, 1987: 140, fig. 1, pls. 4, 5.

Material examined.—Lectotype, male (45.0 by 33.0 mm) (NNM Cru Nr. 1299); Borneo, Kalimantan: Mount Damoes, Sambas, coll. Hallier, Oct 1893. Others—1 female (NHM 1928.12.1.83), Borneo, Sarawak: Kuching, Stebbing Collection, coll. C. Hose. 1 male (NHM 1928.12.1.82), Borneo, Sarawak: Kuching, Stebbing Collection. 1 female (NHM 1880:6), West Borneo, coll. E. Gerrard; 1 female (MZB Cru No. 1986.1257), Borneo, Kalimantan: S. Nagadan, Sanggauledo, Sinkawang, Kal. Sambas, ca. 0°30′N, 109°45′E, coll. F. Sabar & D. Harjono, 8 Sep 1981. 2 females (larger 40.0 by 31.5 mm), 3 males (largest 49.5 by 37.0 mm) (SM Cru Nr. 1986.139–143), Borneo, Sarawak: Simunjan, Upper Simunjan River, 10th Mile Rock Road, foot of Klingkang, ca. 1°22′N, 110°44′E, coll. Loong Tak, Jun 1901. 7 males, 6 females, 4 juveniles (SM Cru Nr 1986.122–138), Borneo, Sarawak: Gunong Matang (present Gunong Serapi), 1°33′16″N, 110°12′51″E, ca. 1000 m asl, Mar 1901. 2 females (ZRC 1997.789), Borneo, Sara-

wak: just outside Fairy Caves (Gua Kapo), 6.8 km from junction of road to Wind Cave and main road, 1°22′55.9″N, 110°7′4.7″E, coll. H. H. Tan & D. C. J. Yeo, 7 Sep 1995. 1 male, 1 female, 1 juvenile (ZRC 1997.801), Borneo, Sarawak: Sg. Kuhas tributary (feeder stream), 0.5 km towards Kg. Lanchang, 6.9 km left at Tebelu Tebakang turnoff, 5.8 km into right trail, 1°9′23.1″N, 110°29′29.9″E, coll. P. K. L. Ng et al., 31 Aug 1996. 3 males, 2 females (ZRC 1984.7037–7041), Borneo, Sarawak: Sadong River, ca. 1°55′N, 113°08′E, coll. Loong Tak, Jan 1901. 3 males, 3 females, 1 juveniles (ZRC 1997.791), Borneo, Sarawak: Sg. Isu, km 20 on road to Simunjan, after branching from Kuching-Sri Aman Road, M. Kottelat, 11 May 1994. 1 male, 1 female, 3 juveniles (ZRC 1997.787), Borneo, Sarawak: Sg. Semabang, ca. km 22 on road to Simunjan, after it branches from road Kuching-Sri Aman, 1°12′52.0″N, 110°55′38.7″E, M. Kottelat, 11 May 1994. 3 males, 1 female (ZRC 1997.790), Borneo, Sarawak: Sg. Kuhas, 1°9′10.0″N, 110°29′22.7″E, P. K. L. Ng et al., 14 Jan 1996.

Diagnosis.—Carapace appearing squarish to wider than long, dorsal surfaces flat, regions slightly rough but not strongly rugose; anterolateral margins convex; epibranchial tooth very prominent, sharp, separated from external orbital angle by distinct V-shaped cleft; external orbital angle triangular, tip level with frontal margin. Ischial sulcus on third maxilliped shallow. Dactylus of last ambulatory leg short. G1 straight or slightly sinuous, terminal segment straight, tip dilated to form rounded flap.

Remarks.—The taxonomic problems, infraspecific variation and general biology of this species have already been discussed in detail by Ng (1987), who argued that the type series (a male and a female from two different localities) of De Man (1899) was heterogeneous, and designated the male as the lectotype.

The third maxilliped exopod of *I. consobrinum* is the most narrow of the known *Isolapotamon* species and the outer margin is also less convex. The ischial groove on the third maxilliped is also very shallow. Whether these characters (and perhaps the G1 as well) justify separating *I. consobrinum* out into a separate genus remains to be evaluated.

Other than recent material from Sarawak which expands its distribution in western Sarawak, there are no new observations to add to Ng's (1987) comments of this species.

Isolapotamon doriae (Nobili, 1900)
Figs. 5I–L, 4

Potamon (*Potamon*) *doriae* Nobili, 1900: 501.

Potamon sp.—Shelford, 1916:265.

Potamon (*Potamon*) *doriae.*—Rathbun, 1904:268.

Isolapotamon mahakkamense.—Bott, 1970b:193 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *mahakkamense.*—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon doriae.—Ng, 1987:143, fig. 2A–G, pl. 6.

Isolapotamon sp.—Ng, 1987:148, fig. 3I–K.

Material examined.—Holotype, male (55.0 by 42.0 mm) (MGE III 228), Sarawak, coll. G. Doria & O. Beccari, between 1865 and 1868. Others—2 males, 3 females, 5 juveniles (SM Cru Nr. 1986.102–111), Penrissen Mountains, Sarawak, 1°16′20″N, 110°08′10″E, coll. R. Shelford, May 1899. 1 male (SM Cru. Nr. 1986.112), Penrissen Mountains, Sarawak, 1°16′20″N, 110°08′10″E, ca. 1000 m, coll. R. Shelford, May 1899.

Diagnosis.—Carapace dorsal surfaces slightly convex, distinctly rugose on lateral regions; anterolateral margins convex, appearing serrated due to strong oblique striae; epibranchial tooth sharp, distinct; outer margin of external orbital

Fig. 4. *Isolapotamon doriae*. Holotype male (55.0 by 42.0 mm) (MGE III 228.9).

angle convex. Dactylus of last ambulatory leg long. G1 very long, gently sinuous, terminal segment sinuous, tip slightly dilated, rounded.

Remarks.—Ng (1987) resurrected the poorly known *I. doriae* after comparing the type material with specimens from the Penrissen Mountains in the Sarawak Museum. Although the G1 terminal segment of this species is quite similar to that of *I. consobrinum*, the external features are so different that there is no doubt that two separate species are involved. Details of the taxonomy of this species can be found in Ng (1987).

Ng (1987), on examining a young specimen of *Isolapotamon* from the Penrissen Mountains collected with the material of *I. doriae*, could not refer it to any known species from Sarawak at that time. We have reexamined the juvenile specimens and now believe that they are conspecific with *I. doriae*. Slight differences observed in the shape of the G1 are probably due to intraspecific variation.

Isolapotamon griswoldi (Chace, 1938)
Fig. 5M–P

Potamon (*Thelphusa*) *consobrinum.*—Borradaile, 1900:94 (not *Potamon consobrinum* De Man, 1899).

Potamon griswoldi Chace, 1938:9.

Potamon (*Potamon*) *griswoldi.*—Yang, 1979:17.

Isolapotamon (*Isolapotamon*) *griswoldi.*—Bott, 1968:120, fig. 2.

Isolapotamon griswoldi.—Bott, 1970b:192, pl. 41 fig. 78, pl. 56 fig. 78.

Material examined.—Paratypes, 3 males (ZRC 1965.12.7.1, ZRC 1990.463–464), Borneo, Sabah: Mt. Kinabalu, Bundutan, Luidan River coll. J. A. Griswold Jr., 1 Jul 1937. Others—3 males, 3 females, 2 juveniles (ZRC 1984.7050–7057), 6 males, 3 female, 3 juveniles (ZRC 1984.7668–

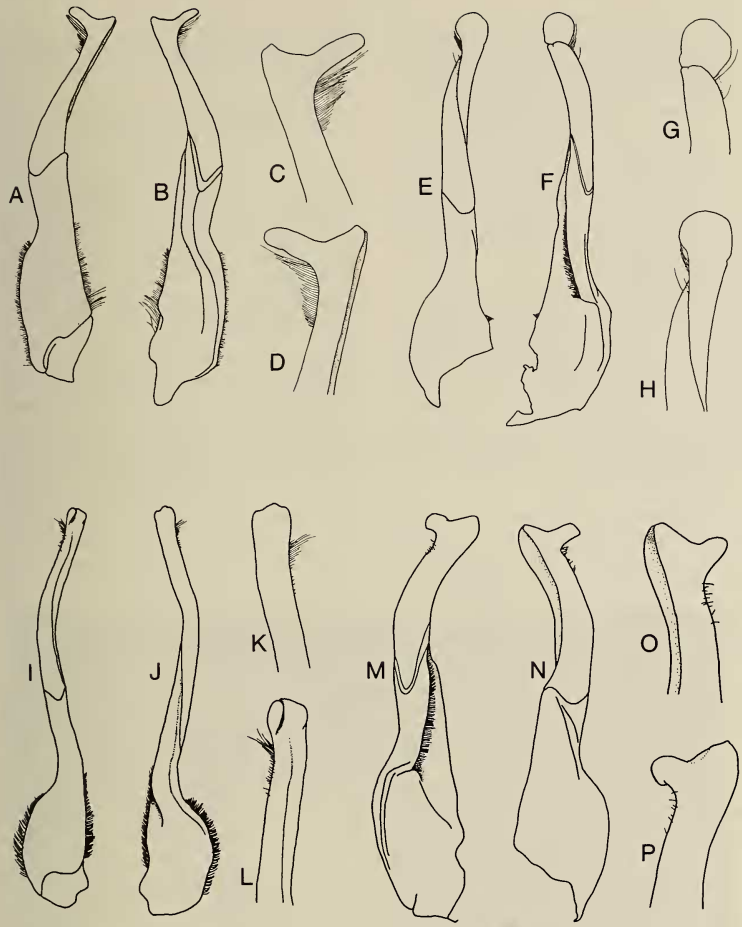

Fig. 5. G1s. A–D: *I. collinsi*, male (ZRC 1997.792); E–H: *I. consobrinum*, lectotype male (NNM Cru. Nr. 1299); I–L: *I. doriae*, holotype male (MGE III 228); M–P: *I. griswoldi*, male (ZRC 984.7050). A, E, I, M: dorsal view; B, F, J, N: ventral view; C, G, K, O: dorsal view, tip of terminal segment; D, H, L, P: ventral view, tip of terminal segment.

7679), 1 male, 1 female (MZB Cru No. 1144), Borneo, Sabah: Mt. Kinabalu, Kadamaian (Kadamayan) River, ca. 6°22′N, 116°26′E, coll. R. Hanitsch, 1900. 1 male (immature), 2 females (CMZ Reg. Nr. 11.1.00), Borneo, Sabah: Mt. Kinabalu, Kadamaian River, ca. 6°22′N, 116°26′E, ca. 630 m asl, coll. R. Hanitsch, 26 Mar 1899. 2 juveniles (ZRC 1997.783), Borneo, Sabah: Kinabalu National Park, Sg. Silan-Silan, near headquarters, under rocks, P. K. L. Ng, 26 Dec 1992.

Diagnosis.—Carapace slightly convex, surfaces slightly rugose; epibranchial tooth distinct, sharp; external orbital angle triangular, outer margin convex. Dactylus of last ambulatory leg short. G1 gently sinuous, terminal segment bifurcated, subequal in length to subterminal segment, distal part bifurcated, subdistal process subequal to distal process.

Remarks.—*Isolapotamon griswoldi* was described by Chace (1938) from several hundred specimens collected by J. A. Griswold Jr. in 1937 from Mt. Kinabalu in Sabah. The species is easily characterised by its G1 terminal segment which resembles a horse's head. The subdistal process is stout, the tip sloping, and the distal process is very stout and rounded. The propodus of the last pair of ambulatory legs is also very broad and the dactylus short.

Chace (1938) in describing *I. griswoldi* suggested that specimens identified as "*Potamon consobrinum*" by Borradaile (1900) may in fact be conspecific with his species. Hanitsch (1900) recorded these specimens as being present in the then Raffles Museum, but they were probably given to the CMZ where Borradaile was based. The first author has examined Borradaile's specimens of "*Potamon consobrinum*" in the CMZ and Chace's suspicions are verified. Although the male is still very young (its G1 is poorly developed) the other morphological features of all three specimens are identical to *I. griswoldi*.

Isolapotamon griswoldi is one of the three species of *Isolapotamon* found in and around the vicinity of Mount Kinabalu, the highest mountain in Borneo; the other two being *I. anomalum* and *I. kinabaluense*.

Isolapotamon grusophallus
Ng & Yang, 1986
Fig. 6A–D

Potamon (*Potamon*) *sinuatifrons.*—Yang, 1979:18 (not *Thelphusa sinuatifrons* H. Milne Edwards, 1853).

Isolapotamon grusophallus Ng & Yang, 1986:15, fig. 1.

Isolapotamon grusophallus.—Ng, 1987: 147, fig. 3G–H, pl. 10.

Material examined.—Holotype, 1 male (42.5 by 31.0 mm) (ZRC 1984.7044), Sarawak, coll. native collector, 1902.—Paratypes—2 females (larger 71.0 by 53.9 mm) (ZRC 1984.7045–7046), 1 female (SM), same data as holotype.

Diagnosis.—Carapace smooth to slightly rugose, lateral regions rugose; anterolateral margins distinctly convex, serrated; epibranchial tooth small, barely separated from triangular external orbital angle. Dactylus of last ambulatory leg long. G1 sinuous, terminal segment sinuous, tip bifurcated, subdistal process long, twice length of distal process.

Remarks.—*Isolapotamon grusophallus* is closest to *I. collinsi*. It is unfortunate that the exact locality where *I. grusophallus* was collected is not known, the only data on the label being somewhere in Sarawak. The details of its taxonomy can be found in Ng & Yang (1986) and Ng (1987).

Isolapotamon ingeri, new species
Figs. 6E–H, 7

Isolapotamon sp.—Ng & Goh, 1987:328, pl. 3, D.

Material examined.—Holotype, male (44.3 by 33.3 mm) (ZRC 1997.796), Borneo, Sabah: Tawau, Tawau Hills Park, Sg. Tawau, coll. Paul Yam, 14 Dec 1991. Paratypes—1 female, (41.4 by 31.0 mm) (ZRC 1997.797), same data as holotype. Others—

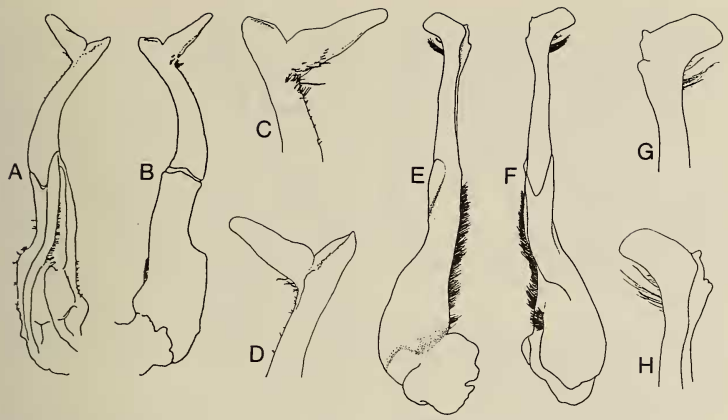

Fig. 6. G1s. A–D: *I. grusophallus*, holotype male (ZRC 1984.7044) (after Ng, 1986); E–H: *I. ingeri*, holotype male (ZRC 1997.796). A, E: dorsal view; B, F: ventral view; C, G: dorsal view, tip of terminal segment; D, H: ventral view, tip of terminal segment.

Fig. 7. *Isolapotamon ingeri*, new species. Holotype male (44.3 by 33.3 mm) (ZRC 1997.796).

1 male (57.4 by 44.8 mm) (ZRC 1997.798), Borneo, Sabah: Lahad Datu, Sg. Palum Tambum, near Danum Valley Field Centre, coll. K. Martin-Smith, Aug 1996. 1 female (ZRC 1989.3419), Borneo, Sabah: Lahad Datu, Madai Caves, Sg. Madai, coll. 27 Jan 1985. 5 males, 1 female (ZRC 1997.799), Borneo, Sabah: near Danum Valley Field Centre, Tambun, Sg. Palum, coll. K. M. Martin-Smith, 9 Oct 1996. 1 male (ZRC 1997.802), Borneo, Sabah: Tawau, Jalan Madai, Gua Madai, Sg. Matarid, 4°43′8.7″N, 118°9′14.7″E, H. H. Tan et al., 6 Oct 1996.

Diagnosis.—Carapace wider than long, relatively smooth; anterolateral margins convex, carinate; epibranchial tooth distinct; external orbital angle acute. Dactylus of last ambulatory leg short. G1 relatively straight, terminal segment subequal to subterminal segment, tip enlarged and flattened, forming rectangular structure.

Description.—Carapace wider than long, surface flat, relatively smooth with numerous small pits; anterolateral margins convex, gradually merging with posterolateral margins; posterolateral margins straight, converging towards posterior margin, posterior margin straight; branchial regions slightly inflated, epigastric groove shallow to indistinct, cervical groove shallow, H-shape depression distinct; epigastric region lightly granulated, epigastric cristae distinct, subparallel to frontal margin, epigastric lobes rectangular, in front of postorbital cristae; postorbital cristae prominent, relatively parallel to frontal margin, not confluent with epigastric cristae or base of epibranchial teeth; frontal margin raised, forming a cristae anteriorly, sinuous, about one-quarter of carapace width, forming four lobes, with two median lobes being wider than lateral lobes; outer orbital angle acute. Anterolateral margin evenly carinate, striated with distinct epibranchial incision. Eyes well developed; supra- and infraorbital cristae prominent, granulated; suborbital regions granulated. Pterygostomial region smooth. Median frontal triangle absent.

Third maxillipeds cover entire oral field, except efferent opening; ischium with longitudinal median groove; exopod with well developed flagellum.

Chelipeds unequal, ventral surface of merus with two distinct cristae, anterior cristae distinctly granulated, posterior cristae less granulated; frontal surface of cheliped with numerous low ridges on lower part, arranged obliquely. Finger of cheliped with shallow grooves.

Ambulatory legs normal, merus without subterminal spine, second pair longest, dactylus of last pair relatively short.

Male abdomen triangular and elongate, widest at third segment, narrows gradually towards telson.

G1 relatively straight, terminal segment subequal to the subterminal segment; tip of terminal segment flattened, forming a rectangular structure. G2 relatively straight, bent at a slight angle at proximal one quarter of terminal segment, tip pointed. Terminal segment slightly shorter than subterminal segment.

Remarks.—Ng & Goh (1987) reported an unidentified *Isolapotamon* from Madai caves in Lahad Datu. We have compared this specimen with the type series of *I. ingeri* and they agree very well in all external asexual characters. *Isolapotamon ingeri* appears to be restricted to the northeastern part of Borneo, being found from Tawau Hills Park, Madai Caves, Danum Valley Conservation Area and Lower Segama River. All these localities are in Sabah.

The shape of the G1 of *I. ingeri* affiliates it with *I. kinabaluense* and *I. anomalum.* It can be differentiated from *I. kinabaluense* by having the distal part of the terminal segment rectangular in shape (vs. "club-like") and subterminal segment without a distinct notch at the proximal end (vs. notch present). *Isolapotamon ingeri* can be differentiated from *I. anomalum* by having the distal side of the G1 tip shorter than the proximal side (vs. distal side longer than proximal side).

Etymology.—We take great pleasure in

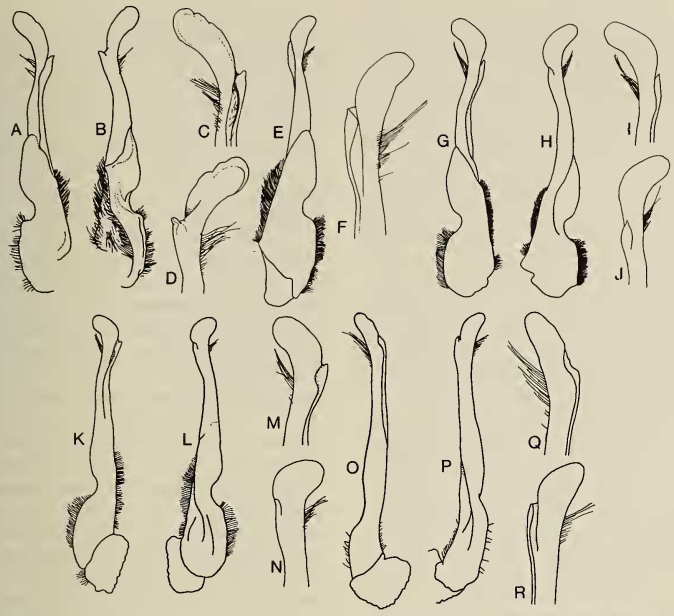

Fig. 8. G1s. of *Isolapotamon kinabaluense* showing variation. A–D: male (41.1 by 30.6 mm) (ZRC 1990.450, Sabah); E–F: same specimen as previous, right G1; G–J: male (40.1 by 30.2 mm) (MCZ 10066, Sabah: Mt. Kinabalu, Kadamayan river); K–N: male (28.0 by 21.0 mm) (ZRC 1997.786, Sabah: Keningau, Sg. Kouran); O–R: male (24.8 by 19.0 mm) (ZRC 1990.449, Sabah: Kota Marud district, Marak Parak, Sg. Surinsin). A, G, K, O: left G1, dorsal view; B, H, L, P: left G1, ventral view; C, I, M, Q: tip of left G1 terminal segment, dorsal view; D, J, N, R: tip of left G1 terminal segment, ventral view; E: right G1, dorsal view; F: tip of right G1 terminal segment, ventral view.

naming this crab after an old friend, Robert F. Inger for helping us collect so many interesting Bornean freshwater crabs over the years.

Isolapotamon kinabaluense
(Rathbun, 1904)
Fig. 8

Potamon (*Potamon*) *kinabaluensis* Rathbun, 1904:269, fig. 9, pl. 10 fig. 2.
Potamon kinabaluensis.—Chace, 1938:13, fig. 2.
Potamon (*Potamon*) *kinabaluensis.*—Yang, 1979:17.
Isolapotamon (*Isolapotamon*) *kinabaluensis.*—Bott, 1968:120, fig. 3.
Isolapotamon kinabaluensis.—Bott, 1970b: 193, pl. 41 fig. 80, pl. 56 fig. 80.

Material examined.—Syntype, 1 female (USNM 29990), Borneo, Sabah: Kinabalu, coll. Whitehead. Others—1 male, 1 female (USNM 75900), Borneo, Sabah: Mt. Kinabalu, Bundutan, coll. Asiatic Primate Expedition, 15 Jul 1937. 1 male (42.2 by 31.6 mm) (MCZ 10065), Borneo, Sabah: Mt. Kinabalu, Bundutuan, Luidan River (G1 figured by Chace 1938), coll. J. A. Gris-

wold Asiatic Primate Expedition, 15 Jul 1937. 1 male (24.2 by 18.8 mm), 1 female (MCZ 10065), Borneo, Sabah: Mt. Kinabalu, Bundutuan, Luidan River, coll. J. A. Griswold, Asiatic Primate Expedition, 15 Jul 1937. 7 male (MCZ 10065), Borneo, Sabah: Mt. Kinabalu, Bundutuan, Luidan River, coll. J. A. Griswold Asiatic Primate Expedition, 15 Jul 1937. 1 male (39.7 by 30.1 mm) (MCZ 10066), Borneo, Sabah: Mt. Kinabalu, Kadamaian (Kadamayan River), ca. 6°22′N, 116°26′E, coll. J. A. Griswold Asiatic Primate Expedition, Nov 1937. 1 male (41.0 by 30.9 mm), 2 female (ZRC 1990.450–452), Borneo, Sabah: Sg. Kindingan, Marak, Parak, Kota Marudu District, ca. 6°17′N, 116°43′E, coll. R. B. Stuebing, 11 Nov 1988. 1 male (25.0 by 19.0 mm) (ZRC 1990.449), Borneo, Sabah: Kota Marudu, Marak Parak, Sg. Sorinsim, rapids, rock bottom, ca. 6°17′N, 116°43′E, coll. R. F. Inger & F. L. Tan, 9 Nov 1988. 1 male (16.5 by 13.1 mm), 1 juvenile (ZRC 1990.453–454), Borneo, Sabah: Tenom, Melalap, Sg. Malutut, 14.5 km north of Tenom, ca. 5°13′N, 115°58′E, coll. R. F. Inger & F. L. Tan, 20 Nov 1988. 1 female (ZRC 1990.455), Borneo, Sabah: Tenom, Crocker Range, Melalap, Sg. Malutut, in tire rut of temporary road, 300 m asl, ca. 5°13′N, 115°58′E, coll. R. B. Stuebing, 1 Dec 1988. 1 female (ZRC 1990.456), Borneo, Sabah: Kota Marudu, Marak Parak, Sg. Tahobang, tributary of Sg. Sorinsim, coll. UKM Sabah, 1988; 1 male (ZRC 1997. 786), Borneo, Sabah: Sg. Kouran, coll. 30 Jan 1991. 4 males, 1 female, 13 juveniles (ZRC 1997.800), Borneo, Sabah: Keningau, Sg. Kouran, coll. 31 Jan 1991. 1 female (42.0 by 33.1 mm) (ZRC 1965.12.7.12), Borneo, Sabah: Bundutan (Bundu Tuhan), Luidan River, ca. 5°58′N, 116°32′E, coll. J. A. Griswold Jr., 15 Jul 1937. 1 male, 1 female (ZRC 1990.465–466), Borneo, Sabah: Bundutan, Luidan River, coll. J. A. Griswold Jr., 15 Jul 1937

Diagnosis.—Carapace slightly convex; epibranchial tooth low but distinct, sharp; anterolateral margin gently serrate; external orbital angle triangular, tip level with frontal margin, outer margin straight. Dactylus of last ambulatory leg long. G1 almost straight, distal part of G1 terminal segment dilated to form "club-like" structure, tip tapering, outer margin of dilated part meeting inner margin at sharp angle, inner margin of distal part projects inwards to form distinct hump.

Remarks.—Rathbun (1904) described this species from three females collected by M. Whitehead in Mount Kinabalu. However, she did not designate any holotype. Since the identification of *Isolapotamon* species is highly dependent on the male G1, we felt that the designation of a lectotype in the present instance is unnecessary. In any case, the syntype female in the USNM agrees well with the other specimens of *I. kinabaluense* we have seen. Chace (1938), while studying the specimens collected by J. A. Griswold Jr. from the Mount Kinabalu area was the first to provide a figure and detailed redescription of this species, including the G1. The ZRC has a large female specimen from the Griswold collection donated by the MCZ in the days of the Raffles Museum (ZRC 1965.12.7.12). This female has the original number of MCZ No. 10065, and the label indicated that there was also a male specimen. The whereabouts of this male is not known. It was probably sent to Bott by the Raffles Museum (M. W. F. Tweedie, pers. comm.) and used by him in his studies (Bott 1968, 1970b). Bott (1970b) lists a male (SMF 2841) from exactly the same locality as the ZRC female, and he had probably retained the Raffles Museum specimen in the SMF. Through the kindness of Dr. A. Johnston, the ZRC has since obtained another pair of *I. kinabaluense* from the Griswold collection (ZRC 1990.465–466) from MCZ by exchange.

The G1 terminal segment of *I. kinabaluense* is quite characteristic. The terminal and subterminal segments are generally in a straight line, the entire G1 being only slightly sinuous. The distal part of the terminal segment is expanded into a broad flap

which varies in shape slightly. The form of the flap is consistent for all the male specimens examined from Luidan River, the type locality; whereas those from the Kadamayan River (MCZ 10066) and Sungai Kindingan (ZRC 1990.450) have a slightly but distinctly different shape. The shapes of the flaps can vary considerably depending on the angle which they are viewed (care was taken to use the same angle of view in this study). The flaps of specimens from the Luidan River are broader; that from Sungai Kindingan the most slender; with the flap from the Kadamayan specimen being approximately intermediate (Fig. 8). The flap-like distal part of the terminal segment is actually an extension of the ventral fold, the dorsal fold ending at the base of the flap as a short, blunt projection, sometimes so low as to appear hump-like. The dorsal and ventral folds are connected by a stiff sloping membrane which extends from the base of the flap to the dorsal fold projection (or hump). This membrane is visible only from the dorsal view. The G2 distal segment protrudes from beneath this membrane, which is the distal part of the G2 groove. The dorsal projection appears as a sharp knob on the dorsal margin, just below the flap-like expansion at the distal part of the terminal segment in Bott's (1968) figure of the G1 of a male of *I. kinabaluense*. This knob is absent in Chace's (1938) specimen and figure, the projection being hump-like instead. All the G1s examined from the Luidan River specimens have a blunt, hump-like dorsal projection. Those from the Kindingan (Fig. 8A–D) and Kadamayan (Fig. 8G–J) rivers have more produced projections. A juvenile G1 is also figured (Fig. 8O–R) for comparison.

For the moment, considering the few specimens from the Kindingan and Kadamayan rivers, the differences noted in the form of the flap and dorsal fold projections with the Luidan River specimens are not regarded as significant supraspecifically. All other features of the G1, as well as the external characters in specimens from all three areas are constant.

There is also often a distinct small dorsal hump at the base of the terminal segment formed by the subterminal segment. This hump is pronounced in most specimens. *Isolapotamon anomalum* is not known to have this feature, whereas it varies somewhat for *I. griswoldi*. It is also present in *I. borneense*, and does not appear to be very useful as a taxonomic character.

The specific name of the species should be "kinabaluense", not "kinabaluensis", since the gender of the genus is neuter.

Isolapotamon mahakkamense
(De Man, 1899)
Fig. 9

Potamon (*Potamon*) *mahakkamense* De Man, 1899:92, pl. 12 fig. 8.

Potamon (*Potamon*) *mahakkamensis*.—Rathbun, 1904:268 (part).

Material examined.—Lectotype, female (61.0 by 45.0 mm) (NNM Cru Nr. 1300), Borneo: Kalimantan, Upper Mahakkam, Bloe-oe, coll. Nieuwenhuis.

Diagnosis.—Carapace surfaces very rugose, covered with numerous small granules, outer margin of external orbital angle slightly longer than inner margin, appearing almost smooth. Closed fingers of larger cheliped without wide gape. G1 not known.

Remarks.—This species is known only from one large female and has not been reported since the original description. Although the G1 of *I. mahakkamense*, is not known, it is nevertheless a distinctive species on the basis of its external morphology. Its highly granulated lateral regions and convex posterolateral margins gives the species a very distinctive appearance. The species closest to *I. mahakkamense* is *I. bauense*. Specimens identified as this species by Bott (1968, 1970b) were referred to *I. bauense* by Ng (1987). See remarks under *I. bauense* for a detailed discussion.

De Man (1899) in his description of this species did not designate a holotype but he

Fig. 9. *Isolapotamon mahakamense*. Lectotype female (61.0 by 45.0 mm), (NNM Cru Nr. 1300).

probably had only one specimen. The present specimen (NNM 1300) is hereby designated as the lectotype of this species.

Isolapotamon mindanaoense
(Rathbun, 1904)
Fig. 10A–D

Potamon (*Potamon*) *mindanaoensis* Rathbun, 1904:268, fig. 8, pl. 10 fig. 5.
Isolapotamon (*Isolapotamon*) *mindanaoense*.—Bott, 1968:121, fig. 5.
Isolapotamon mindanaoense.—Bott, 1970b:192, pl. 41 fig. 79, pl. 56 fig. 79.

Material examined.—Holotype, male (30.5 by 24.0 mm) (MNHN-B 5297), Philippines, Mindanao, coll. M. Montano. Others—5 males (largest 38.1 by 28.8 mm), 13 females (largest 41.9 by 31.3 mm), 3 juveniles (USMN 46985), Philippine Islands, coll. G. A. Mearne. 2 ex. (USNM 032110), Philippines, East Mindanao: Gulf of Davao, Tibuan River.

Diagnosis.—Carapace broader than long; anterolateral margin gently serrated; frontal margin sinous, median lobes slightly forward of lateral lobes; epibranchial regions striated; epigastric cristae forward of postorbital cristae; epibranchial tooth small, separated from external orbital angle by small notch. Chela dorsal surface rugose, smooth ventrally. Telson broader than long. G1 relatively straight, outer margin slightly sinuous, especially on terminal segment, distal part of terminal segment with broad and rounded obliquely directed process. G1 terminal segment tip flap-like, facing outwards.

Remarks.—This species from Mindanao, Philippines, was originally known only from one male type specimen (MNHN-B 5297) (30.5 by 24.5 mm). On a recent sabatical trip to the Smithsonian Museum of Natural History, the first author found a collection of *Isolapotamon* from the Philippines. Examination of the specimens reveals that the G1 and the shape of the abdomen also matches that of *I. mindanaonse* very closely. Unfortunately, the collection locality is stated as Philippines islands. It is therefore still not known whether *I. mindanaoense* extends to other parts of the Philippines.

Isolapotamon mindanaoense is closely related to *I. kinabaluense* especially with regards to the G1. The G1 of *I. kinabaluense* has a prominent flap on the inner side of the

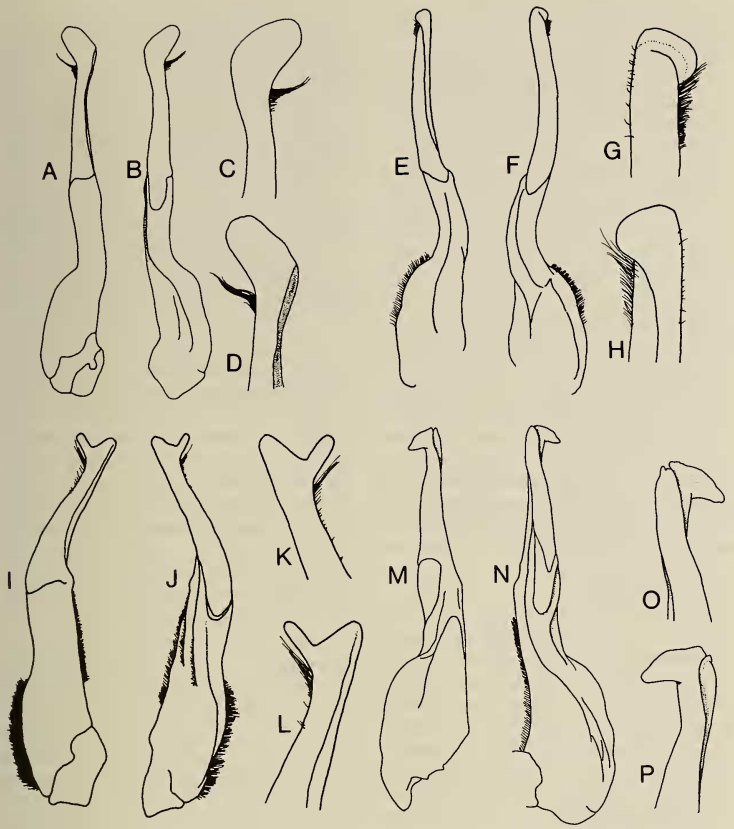

Fig. 10. G1s. A–D: *I. mindanoense*, holotype male (MNHN-B 5297); E–H: *I. naiadis*, holotype male (MZB Cru Nr. 466) (after Ng, 1986); I–L: *I. nimboni*, holotype male (SM Cru Nr 1986.11); M–P: *I. sinuatifrons*, lectotype male (MNHN BP-4353 S). A, E, I, M: dorsal view; B, F, J, N: ventral view; C, G, K, O: dorsal view, tip of terminal segment; D, H, L, P: ventral view, tip of terminal segment.

gonopod whereas the flap is located on the tip of the terminal segment in *I. mindanaoense*. The telson of *I. mindanaoense* is as broad as long. The telson of *I. kinabaluense* is longer than broad. The chela of *I. mindanaoense* possess low flat granules, but is the granules are prominant and distinct in *I. kinabaluense*. The ventral surface of the cheliped carpus is smooth in *I. mindanaoense*. In *I. kinabaluense*, the carpus is rugose.

Isolapotamon mindanaoense can be distinguished from *I. sinuatifrons* and *I. spatha* by the shape of the G1. The G1 terminal segment of *I. sinuatifrons* is twisted

at right angles whereas it is not in *I. mindanaoense*.

The distal part of the G1 terminal segment is more pronounced and longer in *I. mindanaoense*. The distal part is less pronounced and shorter. The carapace of *I. mindanaoense* is more convex and higher, whereas the carapace is lower in *I. spatha*.

Isolapotamon naiadis Ng, 1986
Fig. 10E–H

Isolapotamon naiadis Ng, 1986:216, Figs. 1, 2.

Material examined.—Holotype, male (51.6 by 39.3 mm) (MZB Cru Nr. 466), Borneo, Kalimantan: Njapa Mountains, 1°51′26″ N, 117°17′58″ E. coll. S. S. Liem, 27 Oct 1963. Others—2 males (ZRC 1997.785), Borneo, Kalimantan: Bekeleau, Sg. Magang (Setakak), 3°20′29″N, 116° 59′12.5″E, coll. R. Diesel, 6 Sep 1995.

Diagnosis.—Carapace wider than long, flat, surfaces glabrous, postorbital cristae sloping distinctly backwards. Dactylus of last ambulatory leg long. G1 terminal segment long, not distinctly sinuous, tip rounded, slightly dilated.

Remarks.—This species was previously known from only one large specimen. Comparison of recently collected material from East Kalimantan with the holotype indicates that the G1 diagnostic characters used by Ng (1986) are valid. The form of the frontal margin, however, is less reliable, being less "sunken" (relative to the external orbital angles) in the present specimens. In addition to the ZRC specimens, we have also examined another large specimen, which is now in the collections of Rudolf Diesel in Bielefeld, Germany.

This species is only one of the two species known from eastern Kalimantan, the other being *I. beeliae*. Details of its taxonomy can be found in Ng (1986).

Isolapotamon nimboni Ng, 1987
Fig. 10I–L

Potamon sinuatifrons.—Nobili, 1901:4 (not *Potamon sinuatifrons* H. Milne Edwards, 1853).

Potamon (*Potamon*) *consobrinum.*—Nobili, 1903:15 (not *Potamon* (*Potamon*) *consobrinus* De Man, 1899).

Potamon (*Potamon*) *consobrinus.*—Rathbun, 1904:269 (part) (not *Potamon* (*Potamon*) *consobrinus* De Man, 1899).

Potamon (*Potamon*) *sinuatifrons.*—Colosi, 1920:31 (not *Potamon sinuatifrons* H. Milne Edwards, 1853).

Potamon (*Potamon*) *mahakkamense.*—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon nimboni Ng, 1987:144, fig. 2H–L, pl. 7; postscript pg. 150.

Material examined.—Holotype, male (40.5 by 30.0 mm) (SM Cru Nr 1986.11), Borneo, Sarawak: Simmangang, 1°15′N, 111°26′E), Sep 1894. Paratypes—1 male (27.0 by 21.0 mm), 2 females (largest 23.5 by 17.0 mm), 2 juveniles (SM Cru Nr 1986.12–16), same data as holotype. Others—1 male (MUT), same data as holotype (det. as *Potamon* (*Potamon*) *consobrinum* by Nobili 1903b). 1 male (50.1 by 36.2 mm) (ZRC 1997.784), Borneo, Sarawak: Kapit, Rumah Temanggong Koh, coll. loggers of logging company, 10 May 1996.

Diagnosis.—Carapace dorsal surfaces flat, regions very clear; anterolateral regions with numerous short striae; epibranchial tooth low, blunt, separated from external orbital angle by narrow cleft; outer margin of external orbital angle convex. Dactylus of last ambulatory leg long. G1 sinuous, terminal segment bifurcated at distal part, distal and subdistal processes positioned at right angles to each other, subdistal process very slender, subequal in length to distal process.

Remarks.—This species from Sarawak is distinguished primarily on the basis of its characteristic G1, which bears a general resemblance to that of *I. griswoldi*, *I. collinsi* and *I. grusophallus*. A larger specimen (ZRC 1997.784) has since been made available to us and some taxonomic characters are noted herewith.

Isolapotamon nimboni is closest to *I. col-*

linsi. Ng (1987) mentioned that the two can be differentiated mainly by the angle of the processes of the G1 terminal segment, the angle in *I. collinsi* being more obtuse than that of *I. nimboni,* and the subdistal process being shorter than the distal. No other taxonomic characters were offered to differentiate between the two species. However, in larger specimens of *I. nimboni*, this character becomes difficult to use as the distal process is nearly twice as broad as the subdistal process. The subdistal process is about equal in length to the distal process. The angle between the two processes also becomes very difficult to determine with any accuracy. Comparison of specimens of *I. nimboni* and *I. collinsi* reveals the following differences in asexual characters: branchial region of *I. nimboni* is deeply concave on both sides of the carapace whereas it is slightly concave in *I. collinsi*; mesogastric region is flat in *I. nimboni* but inflated in *I. collinsi*; *I. nimboni* possess glabrous ambulatory legs, whereas the ambulatory legs of *I. collinsi* is pubescent.

Isolapotamon sinuatifrons (H. Milne Edwards, 1853)
Figs. 10M–P, 11

Thelphusa sinuatifrons H. Milne Edwards, 1853:211; A. Milne Edwards, 1869: 167, pl. 10, fig. 2.
Thelphusa sinuatifrons. (?) var.—Miers, 1886:214, pl. 18, fig. 1.
Telphusa sinuatifrons.—De Man, 1892: 296; Bürger, 1894: 2.
Potamon sinuatifrons.—De Man, 1898:404.
Potamon (*Potamon*) *sinuatifrons.*—Rathbun, 1904:266, pl. 10 fig. 9; De Man, 1899:92, 100, pls. 8, 9 fig. 9.
Potamon mindanaoensis.—Balss, 1937: 162, fig. 22.
Isolapotamon (*Isolapotamon*) *sinuatifrons.*—Bott, 1968:121, fig. 6.
Isolapotamon sinuatifrons.—Bott, 1970b: 192, pl. 41 fig. 83.

Material examined.—Lectotype, male (53.0 by 39.0 mm) (MNHN BP-4353 S) (listed as *Potamon sinuatifrons*), male, G1 and G2 only. Paralectotypes—male (abdomen with G1 and G2 attached only) (MNHN BP 3845 S, listed as *Potamon sinuatifrons*). Others—1 male, 1 female (NHM 1884:31), Philippines, Mindanao: Pasauanca, coll. HMS Challenger.

Diagnosis.—Carapace width longer than length, dorsal surface smooth; anterolateral margin with low striae; anterolateral and posterolateral regions striated, striae low; epigastric cristae slightly forward of postorbital cristae; epibranchial tooth distinct, sharp, separated from external orbital angle by distinct V-shaped cleft; frontal margin sinuous; dactylus of last ambulatory legs long. G1 straight, not strongly elongated, distal part of terminal segment with large subdistal process, perpendicular to distal process, appearing "hammer-like".

Remarks.—This species has had a confused taxonomic history, with Bornean species having been confounded with it (Nobili 1901). Ng (1987) showed that the Bornean records of this species belong to *I. nimboni* instead.

The tip of the G1 of *I. sinuatifrons* is closest to *I. griswoldi* from Sabah, but the distal and subdistal processes are more distinctly right-angled in *I. sinuatifrons*. The overall length of the G1 is also proportionately distinctly shorter in *I. sinuatifrons*.

Miers (1886) reported specimens from Pasananca (Mindanao) which apparently differed slightly in their carapace features, but a re-examination of those specimens (NHM 1884:31) revealed that it is *I. sinuatifrons*. Differences observed of the carapace features are variation. Slight differences are also observed in the male G1. The distal part of the G1 terminal segment of the lectotype of *I. sinuatifrons* is twisted and the tip is pointed and faces towards the sternum. Specimens examined from NHM display the twisted distal portion of the G1 terminal segment, but the tip of the terminal segment is rounded and not pointed. This is probably part of the intraspecific variation.

Examination of the photographs of a syn-

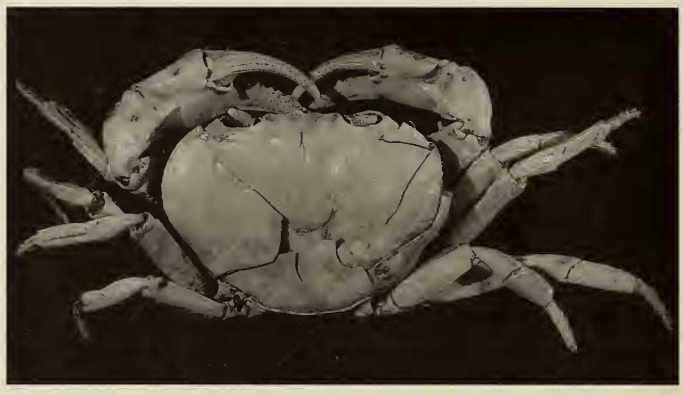

Fig. 11. *Isolapotamon sinuatifrons*. Lectotype male (53.0 by 39.0 mm) (MNHN BP-4353 S).

type male, purportedly from the same expedition as the lecotype, indicates that it differs from photographs of the lectotype in the following characters: the tip of the G1 terminal segment lies flat on the sternum and not twisted, whereas it is twisted and facing towards the sternum in the lectotype; the syntype male has a proportionately shorter ambulatory merus; the left ambulatory leg propodus of the syntype male is proportionately half as short as that on the lectotype; there are four low spines on the posterior margin of the ambulatory propodus of the syntype male but it is smooth in the lectotype; and the syntype male has relatively flatter branchial regions. It is very possible that this specimen in fact represents a separate species. But in the absence of fresh material and more characters, we regard this specimen tentatively as *I. sinuatifrons*.

The type specimens were collected by the Voyage de la Zélée. This makes the locality of the type specimens uncertain as the voyage collected specimens from various localities in Southeast Asia. Specimens from NHM that we had examined were collected in Mindanao, Philippines.

Isolapotamon spatha Ng & Takeda, 1992
Fig. 12A–D

Isolapotamon spatha Ng & Takeda, 1992: 163, fig. 7.

Material examined.—Holotype, male (28.0 by 22.7 mm) (NSMT-Cr 11225), Kraan, 100 m, Sultan Kradarat Province, Mindanao, coll. Y. Nishikawa, 12 Aug 1985. Paratypes.—1 male (30.6 by 224.3 mm), 1 female (NSMT-Cr 11226), same data as holotype.

Diagnosis.—Carapace dorsal surface flat, smooth; epigastric cristae slightly forward of postorbital cristae; epibranchial tooth distinct, blunt, separated from external orbital angle by deep V-shaped cleft; frontal margin sinuous, finely beaded. G1 gently sinuous, laterally flattened, tip dilated, outer distal part of subterminal segment with broad truncate cleft.

Remarks.—This species is superficially similar to *Isolapotamon consobrinum* but can be distinguished by the presence of only a blunt epibranchial tooth and the structure of the G1. The G1 of *I. spatha* resembles that of *I. kinabaluense* in possessing a club-shaped tip but it does not

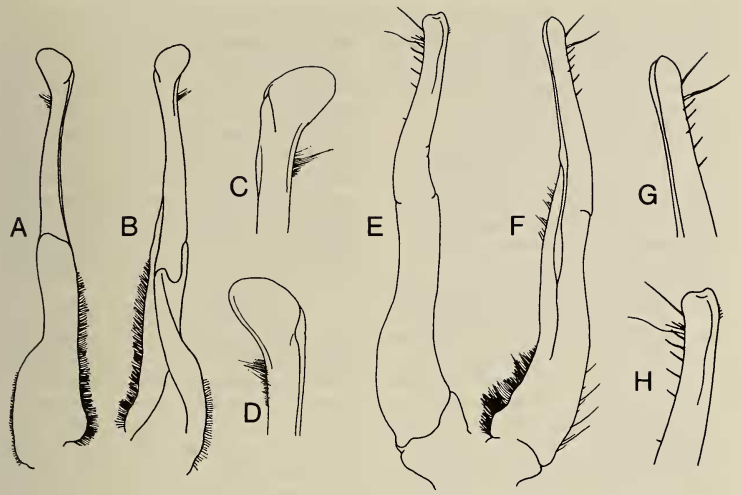

Fig. 12. A–D: *I. spatha*, holotype male (NSMT-Cr 11225) (after Ng & Takeda, 1992); E–H: *I. stuebingi*, holotype male (ZRC 1995.273) (after Ng, 1995). A, E: dorsal view; B, F: ventral view; C, G: doral view, tip of terminal segment; D, H: ventral view, tip of terminal segment.

have a deep concave curvature on the outer distal margin of the subterminal segment. For a more detailed discussion of the taxonomy of this species, see Ng & Takeda (1992).

Isolapotamon stuebingi Ng, 1995
Fig. 12E–H

Isolapotamon stuebingi Ng, 1995:65, figs. 7, 8A–E.

Material examined.—Holotype, male (22.0 by 16.6 mm) (ZRC 1995.273), Borneo, Sarawak: Lanjak-Entimau, Sg. Sekerang, station 90, coll. R. B. Stuebing, 8 Oct 1993. Paratype—male (20.5 by 15.0 mm) (NNM D 4629), Borneo, Sarawak: Lanjak-Entimau Widelife Sanctuary, in stomach of frog (*Rana ibanorum*, Ranidae), coll. C. H. Diong, 17–23 May 1994. Others—1 male (ZRC), Borneo, Sarawak: Sg. Adir (Stn. 5), coll. R. B. Stuebing, 30 Jun 1994.

Diagnosis.—Carapace wider than long, dorsal surfaces flat, regions rugose to granulose, especially lateral region, anterolateral margins distinctly granulated, epibranchial tooth low but distinct, separated from external orbital angle by cleft, external orbital angle broadly triangular. Dactylus of last ambulatory leg short. G1 gently sinuous, terminal segment shorter than subterminal segment, tip subtruncate.

Remarks.—The holotype and all known specimens of *I. stuebingi* are all rather small but the characters used by Ng (1995) to distinguish this species from the closely allied *I. consobrinum* are of diagnostic value even for specimens of comparable sizes.

Discussion

The known distribution of the genus *Isolapotamon* s. str. strongly supports the concept of Wallace's Line which demarcates the Australian and Asian fauna. Of the other two potamid genera in Borneo, *Cer-*

berusa is a wholly cavernicolous taxon (Holthuis 1979) whilst *Ibanum* is probably semi-terrestrial in habits (Ng 1995). *Isolapotamon* is the most speciose genus, and its members extend into Mindanao, but is not known from the Palawan islands or areas further north (Ng & Takeda 1992, 1993). *Isolapotamon* is absent from Sulawesi. In the Tambelan Islands to the west of Borneo, the genus appears to be replaced by the allied *Allopotamon* (Ng 1988b). *Allopotamon tambelanense* (Rathbun 1905), the only species known from the genus, shares many of the external features of *Isolapotamon* (including the form of the third maxilliped exopod) but has a very different G1. As yet, no potamids are known from the Natuna and Anambas islands northwest of Borneo, which might be simply due only to a lack of collecting.

The easternmost species on Borneo appear to be *I. ingeri* whereas *I. consobrinum* is the westernmost taxon. It is striking that there are no species of *Isolapotamon* or any genus even close to *Isolapotamon* in Peninsular Malaysia, Sumatra, Java or the Lesser Sunda Islands. In Borneo, while *Cerberusa* and *Ibanum* are probably sister genera (see Ng 1995), neither seems to be very close to *Isolapotamon*.

The distribution of the various *Isolapotamon* species is also interesting. There are only three known non-Bornean species—*I. mindanaoense, I. spatha* and *I. sinuatifrons*, all from the island of Mindanao in southern Philippines. In the morphology of the G1, two of the Philippine species, *I. mindanaoense* and *I. spatha*, appear to be most closely related to the Sabahan species like *I. kinabaluense* and *I. anomalum*. The overall shape of the G1 is similar to that of *I. kinabaluense*, but the shape and position of the dorsal and ventral folds of the distal part are closer to the condition in *I. anomalum*. The G1 of *I. sinuatifrons* generally resembles that of *I. anomalum*, although the distal dilation of the terminal segment in the former species is positioned at sharply right angles to the rest of the segment. The likelihood that the Mindanao *Isolapotamon* originated from species in northern Borneo thus seems high. The absence of *Isolapotamon* on Palawan is also of interest. Recent collections in Palawan uncovered numerous new species (including a new genus of potamid, *Insulamon* Ng & Takeda, 1992), but no species of *Isolapotamon* (see Ng & Takeda 1992, 1993). Similarly, another genus of potamid, *Ovitamon* Ng & Takeda, 1992, occurs on southern Luzon and the nearby islands in the Philippines (Ng & Takeda 1992).

The richness and diversity of the *Isolapotamon* fauna in Borneo and their restricted distribution in the Philippines (only in Mindanao) seems to indicate that *Isolapotamon* entered Philippines from Borneo. The islands southwest of Mindanao (Sulu Islands) were almost certainly connected to Mindanao during the last ice age in the Pleistocene, and the proximity of these islands to Borneo together with the shallow adjacent seas would have resulted in a land bridge between Mindanao and north Borneo during the last ice age.

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